# Calyptogena (Bivalvia: Vesicomyidae) from Neogene Strata in the Joetsu District, Niigata Prefecture, Central Japan

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*Abstract.* Four species of *Calyptogena* are recorded from the middle Miocene to upper Pliocene in the Joetsu district, Niigata Prefecture, central Japan: *C. pacifica* Dall, *C. cf. nipponica* Oinomikado & Kanehara, *C. sp.* A and *C. sp.* B. This is the first record of *Calyptogena* sp. A in this district. *Calyptogena pacifica* lived in lower sublittoral to bathyal zones while *C. sp.* B may have lived in the bathyal zone. A possible reason why the genus flourished in this district is the reducing deep water environment and methane seepage derived from the oil reservoir.

### INTRODUCTION

The genus *Calyptogena* Dall, 1891 is a characteristic member of modern chemosynthetic communities around deep sea hydrothermal vents, cold seeps and whale carcasses (Smith et al., 1989; Sibuet & Olu, 1998; Tunnicliffe et al., 1998). Cold seep *Calyptogena* species are known from both passive and active margins in the Gulf of Mexico (depth range 400–5000 m), the eastern Pacific from Oregon to Chile (450–5100 m) and the Pacific side of the Japanese Islands (500–6000 m) (Sibuet & Olu, 1998).

Fourteen species of *Calyptogena* have been found in 23 cold seep and 17 hydrothermal vent sites around the Japanese Islands (Kojima, 2002; Okutani et al., 2000). Most of these occurrences are from forearc basins and trenches, and are deeper than 500 m (Higo et al., 1999; Okutani et al., 2000). In contrast, very few *Calyptogena* species have been found in back-arc basins. Examples include *C. pacifica* Dall, 1891 and *C. rectimargo* Scarlato, 1981 in the Okhotsk Sea (Tiba, 1972; Scarlato, 1981) and a number of semi-fossil specimens of *Calyptogena* sp., off Wakkanai, on the Japan Sea side of Hokkaido, in water 60–120 m deep (Majima, 1999; Majima et al., 2000).

No living *Calyptogena* species has been found in the main part of the Japan Sea. However, the genus has extensive fossil records in the region. In the Japan Sea borderland other than the Joetsu District, the following *Calyptogena* species have been recorded from the early middle Mioccne to middle Pleistocene (Amano et al., 2001): *C.* sp., *C. akanudaensis* Tanaka, 1959, *C. uchimuraensis* (Kuroda, 1931), *C. pacifica* and *C. nipponica* Oinomikado & Kanehara, 1938. Their occurrences are confined

to single localities. In contrast, many fossil records of *Calyptogena* have been recorded in the Joetsu District, southwestern part of Niigata Prefecture, central Japan (Figure 1). *Calyptogena pacifica* is known from the upper Miocene Nodani Formation and the Pliocene Kawazume and Nadachi Formations in Joetsu City, central Joetsu District (Kanno et al., 1989; Amano and Kanno, 1991). Amano (1994) illustrated vesicomyids from the upper part of the Pliocene Kurokura Formation in Matsunoyama Town, eastern Joetsu district as *C. nipponica*. Ueda et al. (1995) reported the occurrence of *Calyptogena* sp. from the upper Miocene Ogaya Formation in Kakizaki Town, northeastern Joetsu district, although they did not describe this species taxonomically.

Recently we have collected many additional *Calypto*gena specimens from the Neogene deposits in the Joetsu District including a species hitherto unknown. This paper summarizes all known specimens of *Calyptogena* in the Joetsu District, and discusses why they are so common in this area.

## LOCALITIES AND OCCURRENCES OF CALYPTOGENA

Four species of *Calyptogena* have been found at 16 localities in the Joetsu District (Figure 1): *Calyptogena pacifica* Dall (localities A1–A7, C1), *C. cf. nipponica* Oinomikado & Kanehara (localities C2, E1, E2), *C.* sp. A (localities A8, B1), and *C.* sp. B (localities C3, D1, D2). The localities A1, A2, A4 and A5 correspond to the localities 4, 3, 1 and 2 of Kanno et al. (1989). The localities A2 and A4 are equal to the K20 and N36 of Amano and Kanno (1991) respectively. The locality E1 in Matsunoyama Town is equal to the locality K4 of Amano (1994).



Figure 1. Localities of *Calyptogena* and anticline axis (using the topographical maps of "Takada-seibu," "Takada-toubu," "Myoko-san," "Kakizaki," "Matsunoyama Onsen," scale 1:50,000, published by Geographical Survey Institute of Japan).

The locality D1 corresponds to the locality of C. sp. by Ueda et al. (1995).

Occurrences of the fossils can be grouped into four types as Type I–Type IV (Table 1). Type I is an occurrence in which many disarticulated specimens are found

in black mudstone (locality A1). Type II contains many localities (A2—7, B1, C1, C3, E1) at which one or more articulated specimens occur in mudstone or small (<10 cm) calcareous concretions (Figures 2A, 2C). Type III occurrence is seen at localities A8, C2 and E2 where

### Table 1

Type of occurrences of Calyptogena species in the Joetsu District.  $N^* =$  Number of specimens: A, abundant.

Loc.	Species	N*	Most lithology	Age & Formation				
Type I	Disarticulated specimens							
A1	C. pacifica	А	dark gray mudstone	Pliocene Nadachi F.				
Туре ІІ	Articulated specimens in r	nudstone or si	nall calcareous concretions					
A2	C. pacifica	7	small calcareous concretions	Pliocene Kawazume F.				
A3	C. pacifica	1	dark gray pebbly mudstone	Upper Miocene Nodani F.				
A4	C. pacifica	14	small calcareous concretions	Upper Miocene Nodani F.				
A5	C. pacifica	1	small calcareous concretion	Upper Miocene Nodani F.				
A6	C. pacifica	1	small calcareous concretion	Upper Miocene Nodani F.				
A7	C. pacifica	1	black pebbly mudstone	Upper Miocene Nodani F.				
B1	<i>C</i> . sp. A	2	black mudstone	Middle Miocene Nanbayama F.				
C1	C. pacifica	1	black mudstone	Pliocene Kurokura F.				
C3	C. sp. B	1	black mudstone	Pliocene Kurokura F.				
El	C. cf. nipponica	4	small calcareous concretions	Pliocene Kurokura F.				
Type III	Packed articulated specime	ens in a large	calcareous concretion					
A8	<i>C</i> . sp. A	А	calcareous mudstone (20 cm)	Middle Miocene Nanbayama F.				
C2	C. cf. nipponica	А	large calcareous concretion	Pliocene Kurokura F.				
E2	C. cf. nipponica	А	large calcareous concretion (120 cm)	Pliocene Kurokura F.				
Type IV Articulated specimens in limestone bed								
D1	<i>C</i> . sp. B	А	brecciated limestone bed (20 m in width, 4.5 m in thickness)	Upper Miocene Ogaya F.				
D2	<i>C</i> . sp. B	А	limestone bed (10 m in width, 3 m in thickness)	Upper Miocene Ogaya F.				

many packed articulated specimens are found in large (>10 cm) calcareous concretions (Figure 2D). Type IV occurrence is seen at localities DI and D2 where thick limestone or brecciated limestone beds are formed by many packed articulated specimens (Figure 2B).

Judging from these occurrences, most *Calyptogena* specimens are autochthonous. Despite being disarticulated at localities A1, we interpret these specimens as indigenous because of their lithofacies occurrences and associated fauna. It is significant that *Calyptogena* cf. *nipponica* (localities C2, E1, E2) and *C*. sp. B (localities C3, D1, D2) occur near the axis of an anticline (Figure 1). All material treated in this paper is housed at the Joetsu University of Education (JUE).

#### SYSTEMATIC DESCRIPTION

Family Vesicomyidae Dall and Simpson, 1901

### Genus Calyptogena Dall, 1891

### Calyptogena pacifica Dall, 1891

### Figure 3

Calyptogena pacifica Dall, 1891: 190; Dall, 1895: 713, pl. 25, figs. 4, 5; Grant & Gale, 1931: 278–279, pl. 13, figs. 13a, b; Otuka, 1937: fig.; Otatume, 1942: 435–437, pl. 16, figs. 1–12; Okutani, 1966: pl. 27, figs. 1, 3; Tiba, 1972: 155, pl. 19, figs. 6, 6a; Kanno et al., 1989: figs.

7 1-15; Okutani, 2000: 997, pl. 496, fig. 7; Amano, 2002: 27, figs. 3-4, 3-9; Amano, 2003: figs. 3-14.

- Unio moraiensis Suzuki, 1941: 55-56, pl. 4, figs. 2-5.
- Calyptogena (Calyptogena) pacifica Dall. Bernard, 1974: 11–13, pl. 12, figs. 1A, 2A, 3A, 4A–D; Boss and Turner, 1980: 188–189, figs. Ba–b, Ca–b.

*Vesicomya (Calyptogena) pacifica* (Dall). Coan et al., 2000: 341, pl. 70.

**Type locality:** 322 fathoms from off Dixon Entrance of southeastern Alaska.

### Type specimen: USNM no. 122549 (Holotype).

**Remarks:** Kanno et al. (1989) described the fossils of *Calyptogena pacifica* Dall, 1891 from the Joetsu District in detail. We collected new additional specimens from the Nodani Formation at localities A3, A6, and A7 in Joetsu City, and at locality CI of the Kurokura Formation in Maki Village, eastern Joetsu District. The new and previously described specimens in the Joetsu District are a maximum of 38.1 mm long (Table 2) and are thus smaller than the type, which is 48 mm long and 27 mm high.

In the Joetsu District, *Calyptogena pacifica* is frequently associated with a number of species characteristic of chemosynthetic communities (e.g., *Solemya* spp., *Lucinoma acutilineata* (Conrad), *Conchocele bisecta* (Conrad)), and other bivalves (e.g., *Portlandia lischkei* (Smith) and *Axinopsida subquadrata* (Adams)) (Table 3). In contrast with other species of *Calyptogena* in Joetsu, *C. pa*-



Figure 2. Occurrences of *Calyptogena*. A. Deformed articulated shell of *Calyptogena* sp. A in black shale at the river-side cliff of Loc. B1, in Nanbayama Formation. Both dorsal and ventral margins of shell are nearly parallel to the bedding plane. B. Limestone composed of many specimens of *Calyptogena* sp. B (white arrow) in the cliff of Loc. D2, in Ogaya Formation. C. Articulated *Calyptogena* sp. B in black mudstone at the river-side cliff of Loc. C3, in Kuorokura Formation. The shell occurred in living position, perpendicular to the bedding plane. D. Largest calcareous concretion yielding *Calyptogena* cf. *nipponica* at Loc. E2, in Kurokura Formation.

*cifica* is frequently associated with taxodont bivalves. Based on the present-day depth ranges of *Portlandia lischkei* and *Axinopsida subquadrata*, we suggest that fossil *C. pacifica* in the Joetsu District was living at 100–300 m depth. Amano (2003) also pointed out that this species may have lived on the lower shelf, based on associated fauna and community structure of the late Miocene Morai fauna in Hokkaido. Recently, it has become clear that living *C. pacifica* ranges from 55 to 2200 m in depth (Fujiwara, 2003), which includes the estimated paleoba-thymetry of fossils.

We found a specimen of *C. pacifica* showing an unsuccessful naticid drill hole from locality A3. Amano (2003) also recognized many drilled specimens of *C. pacifica* from the Morai Formation. Amano (2003) suggested *C. pacifica* might have lived at relatively low sulphide



Figure 3–15. *Calyptogena* species from the Joetsu District. Figure 3. *Calyptogena pacifica* Dall, L = 21.3 mm, JUE no. 15744, Loc. A3, Nodani Formation. White arrow shows an unsuccessful drilled hole. Figures 4, 5, 11, 12, 13. *Calyptogena cf. nipponica* Oinomikado and Kanehara (JUE no. 15720): Figure 4. L = 36.1 mm; Figure 5. L = 36.8 mm; Figure 11. L = 27.4 mm; Figure 12. L = 129.3 mm; Figure 13. L = 28.9 mm. Surface is sculptured by fine radial threads; Loc. E2, Kurokura Formation. Figures 6a, b, 9. *Calyptogena* sp. A. (JUE no. 15719): Figure 6a. L = 35.9 mm; Figure 6b. L = 55.7 mm; Figure 9. L = 74.8 mm; Loc. B1, Nanbayama Formation. Figures 7, 8, 14, 15. *Calyptogena* sp. B; Figure 7. Juvenile form, L = 28.8 mm; Figure 8. L = 41.7 mm; Figure 14. L = 89.3 mm; Figure 15. L = 57.2 mm; Loc. D2, Ogaya Formation. Figure 10. *Calyptogena* sp. B, L = 119.8 mm, Loc. C3, Kurokura Formation.

### Table 2

Measurements of *Calyptogena* in the Joetsu District. Many specimens from this district are deformed or partly preserved. Only perfect specimens are measured and shown in this table.

		Length	Height	
Species	Loc.	(mm)	(mm)	H/L
Calyptogena sp. A	A8	86.5	34.3	0.40
	B1	74.8	24.6	0.33
C. sp. B	C3	119.8	35.5	0.30
	C3	32.6	18.7	0.56
	D2	69.6	32.0	0.46
	D2	29.9	12.2	0.41
	D2	28.8	16.6	0.58
	D2	23.2	14.7	0.63
	D2	10.4	6.6	0.64
C. nipponica (Holotype)		115.4	46.1	0.40
C. cf. nipponica	E2	131.9	83.0	0.63
	E2	129.3	64.8	0.50
	E2	89.9	48.7	0.54
	E2	67.8	37.6	0.56
	E2	55.5	32.5	0.59
	E2	38.7	21.3	0.55
C. pacifica (Holotype)	_	48.0	27.0	0.56
C pacifica	A1	36.7	22.6	0.62
er pueljieu	A1	31.8	19.5	0.61
	A1	28.7	17.5	0.61
	A1	23.6	14.7	0.62
	A2	30.9	20.9	0.68
	A3	21.3	12.7	0.60
	A4	26.5	16.4	0.62
	A4	22.0	13.9	0.63
	A5	38.1	23.7	0.62

concentrations in shallower water than other vesicomyids. This might explain why *C. pacifica* is frequently associated with taxodonts rather than other chemosynthetic fauna, and sometimes is bored by naticid or muricid gastropods.

**Distribution:** Late Miocene to Recent. Late Miocene: Morai Formation, Hokkaido (Otatume, 1942; Amano, 2003); Nodani Formation, Niigata Prefecture (Kanno et al., 1989; this study). Pliocene: Kawazume and Nadachi formations, Niigata Prefecture (Amano and Kanno, 1991); Kurokura Formation, Niigata Prefecture (this study). Pleistocene: Wakimoto Formation, Akita Prefecture in northeastern Honshu (Otuka, 1937). Recent: Okhotsk Sea, Bering Sea and off Alaska in 500–700 m of water (Higo et al., 1999); Aleutian Islands to San Diego, California in 550–2000 m of water (Coan et al., 2000); Alaska to South California in 55–2200 m of water (Fujiwara, 2003).

# Calyptogena cf. nipponica Oinomikado & Kanehara, 1938

### Figures 4, 5, 11, 12, 13

Calyptogena nipponica Oinomikado and Kanehara. Amano, 1994: pl. 3, figs. 1, 3, 8, 11.

**Material:** Two specimens (JUE no. 15466) from locality E1 in Matsunoyama Town, six specimens (JUE no. 15720) from locality E2 in Matsudai Town, and one specimen from locality C2 in Maki Village. All specimens are from the upper part of the Pliocene Kurokura Formation.

Description: Shell large in size, up to 131.9 mm long and 83.0 mm high (Table 1), thick, elongate subquadrate, less inflated, inequilateral, sculptured by growth lines and very fine radial threads. Beak situated at anterior onefourth of shell length. Posterior margin subtruncated; anterior margin rounded. Postero-dorsal margin parallel with nearly straight ventral margin. In large specimens, ventral margin slightly concave. Blunt ridge running from beak to postero-ventral corner. Anterior muscle scar distinct and ovate. Pallial sinus slight in small specimens (up to ca. 30 mm length), but pallial line entire in larger specimens. In left valve, hinge plate rather wide, with three cardinal teeth; anterior teeth (2a, b) conjoined at uppermost part forming inverted V-shape, 2b thick and with weak groove on its top; posterior tooth (4b) long and thin, separated from anterior one by deep groove; subumbonal pit shallow behind posterior tooth.

**Remarks:** Based on shell outline, size and age, Amano (1994) identified the specimen from locality E1 as *Calyptogena nipponica* Oinomikado & Kanehara, 1938, a species first described from the Pliocene Ushigakubi Formation in Niigata Prefecture (Figure 4). However, the hinge structure of the holotype of *C. nipponica* is incompletely preserved. This prevents us from definitely identifying the new specimens as *C. nipponica*. Therefore, we refer the new specimens to *C. cf. nipponica*.

When they proposed *Calyptogena nipponica* as a new species, Oinomikado and Kanehara (1938) compared their species with *C. pacifica* Dall, 1891, and *C. elongata* Dall, 1916. However, in its elongate quadrate outline, large size, and many fine threads (Figure 13), *C. cf. nipponica* is more similar to the Recent species *C. solidissima* Okutani, Hashimoto & Fujikura, 1992, than either is to *C. pacifica* and *C. elongata*. *Calyptogena* cf. *nipponica* differs from *C. solidissima* by having a more anteriorly situated beak, a distinct ridge from beak to ventral corner, and a more stout and bifid posterior ramus (2b) of anterior tooth.

*Calyptogena* cf. *nipponica* at localities E1 and E2 occurs with species characteristic of chemosynthetic communities, including *Lucinoma acutilineata* and *Conchocele bisecta*.

### Table 3

Associated fauna of *Calyptogena pacifica*, *C*. cf. *nipponica*, and *C*. sp. B. When only *Calyptogena* specimens occurred, these localities are omitted in this table.

	Calyptogena pacifica					Calyptogena pacifica cf. nipponica		<i>Calyptogena</i> sp. B			
Species	Al	A2	A3	A4	A5	A6	A7	El	E2	C3	D1
Solemya (Acharax) tokunagai Yokoyama	+										
<i>S</i> . sp.		+		+							
Acila sp.							+				
<i>Batlıymalletia inermis</i> (Yokoyama)							+				
Nuculana (Nuculana) pernula (Muller)	+										
<i>N</i> . sp.	+		+								
<i>N.</i> ?sp.										+	
Portlandia (Portlendella) lischkei (Smith)			+								
<i>P</i> . sp.	+						+				
Bathymodiolus sp.											+
Lucinoma acutilineata (Conrad)	+	+							+	+	
L. ? sp.								+			
Conchosele bisecta (Conrad)		+				+			+		
<i>C.</i> sp.	+							+		+	
Axinopsida subquadrata (Adams)							+				
Callocardia ? sp.					+						
Neptunea sp.				+					+	+	
Buccinum sp.								+			

**Distribution:** Pliocene Kurokura Formation, Niigata Prefecture.

# Calyptogena sp. A

# Figures 6a, b, 9

**Material:** Two specimens (JUE no. 15719) from locality B1 in Myoko Village and one specimen (JUE no. 15249) from locality A8 in Joetsu City. All specimens are from the middle Miocene Nanbayama Formation.

**Description:** Shell medium in size, elongate modioliform, less inflated, length 2.5–3.0 times greater than high, very inequilateral, ornamented with growth lines. Beak situated at anterior one-fifth of shell length. Posterior margin more broadly rounded than anterior margin, continues to gently sloping postero-dorsal margin; ventral margin slightly concave. Anterior muscle scar distinct and semi-circular shape. In left valve, hinge plate narrow, with three cardinal teeth; anterior teeth (2a, b) conjoined at uppermost part forming inverted V-shape, separated from posterior long tooth (4b) by deep groove.

**Remarks:** Shell material is absent and thus the inner structure of specimens is unclear. Moreover, shells of this species are slightly deformed or partly preserved. Such poor preservation prevents us from establishing any new species. No associated molluscan species were found with *C*. sp. A.

**Distribution:** Middle Miocene Nanbayama Formation, Niigata Prefecture.

### Calyptogena sp. B

### Figures 7, 8, 10, 14, 15

Calyptogena sp. Ueda et al., 1995: figs. 4a-d.

**Material:** Six specimens (JUE no. 15717) from the upper Miocene Ogaya Formation at locality D2 in Kakizaki Town and two specimens (JUE no. 15744) from the Pliocene Kurokura Formation at locality C3 in Maki Village.

**Description:** Shell large in size, elongate modioliform, moderately inflated, length 3.4 times greater than high in adult shell, very inequilateral, ornamented with growth lines. Beak situated in anterior one-forth of shell length. Postero-dorsal margin gently sloping; ventral margin moderately concave in adult shell. Nymph rather long, occupying two-thirds of postero-dorsal margin. In right valve, hinge plate rather narrow; central tooth (1) nearly vertical; posterior tooth (3b) long and oblique, but anterior tooth (3a) not observed.

**Remarks:** This species may be new to science, but incomplete preservation of the specimens precludes us from naming a new species. The specimens illustrated as C. sp. by Ueda et al. (1995) are immature forms of this species. Immature shells of C. sp. B have an elongate ovate



Figure 16. Relation between shell length and ratio of height to length (H/L %) for *Calyptogena pacifica, C. nipponica, C.* cf. *nipponica, C.* sp. A, and *C.* sp. B.

outline like *C. pacifica* (Figures 7, 16). As they grow, they attain a more elongated shape.

The specimens of *Calyptogena* sp. B resemble *C*. sp. A in their shell outline. However, *Calyptogena* sp. B differs from *C*. sp. A by having a larger size and a strongly concave ventral margin. The adult shells of *C*. sp. B also resemble the recent species *C*. *phaseoliformis* Metivier, Okutani & Ohta, 1986, in having an elongated outline and concave ventral margin. However, *C*. sp. B differs from *C*. *phaseoliformis* in having a more acutely rounded anterior margin. The ontogenetic trend of the shell outline of *C*. *phaseoliformis* is not known as no immature shells have been found.

At locality D1, only *Bathymodiolus* sp. occurs with *C*. sp. B. This is noteworthy as today the shallowest depth *Bathymodiolus* has been found is 680 m (Kurozumi, 2000), suggesting that *C*. sp. B at locality D1 may have lived in water deeper than the upper bathyal zone.

**Distribution:** Late Miocene to Pliocene. Late Miocene: Ogaya Formation, Niigata Prefecture. Pliocene: Kurokura Formation, Niigata Prefecture.

### DISCUSSION

Four species of *Calyptogena* are recorded from many localities in the Joetsu District. Their geological range is from the middle Miocene to the late Pliocene. During this time, *Calyptogena* species lived in fine-grained sediments that were deposited in the water deeper than lower sublittoral zone (Endo and Tateishi, 1990; Amano and Kanno, 1991; Amano, 2002). Judging from the color of the mudstone or shale enclosing fossils and the associated fauna, these sediments were deposited in reducing environments. *Calyptogena pacifica* lived in lower sublittoral to upper bathyal zones while *C*. sp. B may have lived in the bathyal zone as suggested above. Page 210

Area Age		Joetsu	Kakizaki	Maki	Matsudai • Matunoyama
Pleist.					
cene	Late	Nadachi F. •			
Plio	Early	Kawazume F. ●		Kurokura F.	Kurokura F.
	Late	• Nodani F.	Ogaya F. ▼		
Miocene	Middle	Nanbayama F.			
	Early				

# Calyptogena pacifica AC. sp. A V C. sp. B C. cf. nipponica

Figure 17. Stratigraphical occurrences of Calyptogena in the Joetsu District.

Another possible explanation for the diversity and abundant occurrence of Calyptogena species in the Joetsu District may be tectonic setting. It is noteworthy that Calyptogena cf. nipponica and C. sp. B in the Joetsu District are found in the late Miocene to the early Pliocene (Figure 17) because it was at this time that most of the sediments in the back-arc basin were folded (e.g., Kano et al., 1991) and anticlinal oil and gas traps were formed as a result (Hayashi, 1984). Many small oil and methane gas fields are developed near anticlinal axes in the area. These include the Nadachi oil field in Nadachi Town, the Gozu oil field in Joetsu City, the Maki oil field in Maki Village, the Kubiki oil and gas field near Kakizaki Town and the Matsunoyama oil field in Matsunoyama Town (Niigata Prefecture, 1977). Large concretions of C. cf. nipponica at locality E2 and limestone of C. sp. B at localities D1 and D2 occur near the axes of of Yamanaka-Kiriyama (Watanabe, 1938) and Kuroiwa (Yoneyama Research

Group, 1973) anticlines respectively. We surmise that these *Calyptogena* colonies depended on the hydrocarbon-rich fluids emanating near the anticlinal crests. Similar living chemosynthetic communities have been recorded only on the oil-producing region in the Gulf of Mexico (Kennicutt et al., 1985; Callender et al., 1990).

The smallest species in the area, *C. pacifica*, probably lived in shallower water than the other fossil species. There is very little data available based on the occurrences of *C*. sp. A. Both species seem to independent of any obvious geological structure. It is possible, therefore, that neither of them was linked to discrete seep sites, and if so the source of their nutrition is unclear.

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